

Innovation not recovery: dynamic redox promotes metazoan radiations

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ABSTRACT

Environmental fluctuations in redox may reinforce rather than hinder evolutionary transitions, such that variability in near-surface oceanic oxygenation can promote morphological evolution and novelty. Modern, low-oxygen regions are heterogeneous and dynamic habitats that support low diversity and are inhabited by opportunistic and non-skeletal metazoans. We note that several major radiation episodes follow protracted or repeating intervals (>1 million years) of persistent and dynamic shallow marine redox (oceanic anoxic events). These are also often associated with short-lived mass-extinction events (<0.5 million years) where skeletal benthic incumbents are removed, and surviving or newly evolved benthos initially inhabit transient oxic habitats. We argue that such intervals create critical opportunities for the generation of evolutionary novelty, followed by innovation and diversification.

We develop a general model for redox controls on the distribution and structure of the shallow marine benthos in a dominantly anoxic world, and compile data from the terminal Ediacaran–mid-Cambrian (~560–509 Ma), late Cambrian–Ordovician (~500–445 Ma), and Permo-Triassic (~255–205 Ma) to test these predictions. Assembly of phylogenetic data shows that prolonged and widespread anoxic intervals indeed promoted morphological novelty in soft-bodied benthos, providing the ancestral stock for subsequently skeletonized lineages to appear as innovations once oxic conditions became widespread and stable, in turn promoting major evolutionary diversification. As a result, we propose that so-called ‘recovery’ intervals after mass extinctions might be better considered as ‘innovation’ intervals.

Key words: anoxia, innovation, recovery, mass extinctions, radiations.

CONTENTS

I. Introduction	1
II. Low-oxygen habitats: ecology and evolution	2
(1) Ecological dynamics of modern oxygen minimum zones	2
(2) A model for evolutionary dynamics during intervals of prolonged anoxia	3
III. Anoxia and radiations	4
(1) Ediacaran anoxia and the Cambrian radiation	4
(2) Late Cambrian anoxia and the Ordovician radiation	5
(3) Permo-Triassic extinction and Triassic radiation	7
IV. Conclusions	9
V. Acknowledgements	9
VI. References	9

I. INTRODUCTION

Dramatic perturbations of the carbon cycle appear to create the conditions for evolutionary diversification: indeed, evolutionary theory predicts that environmental fluctuations

can often reinforce evolutionary transitions (Boyle & Lenton, 2006). Sustained declines in Phanerozoic global diversity correlate with low extinction rates immediately after mass extinctions, and very high extinction rates tend to be followed by equally high origination rates (Alroy, 2008) (Fig. 1A).

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Mass extinctions in particular, which are short-lived events [<0.5 million years (Myr)], result in profound taxonomic and ecological restructuring of the biosphere (Krug, Jablonski & Valentine, 2009; Knope *et al.*, 2015). The Earth system post-extinction, often lasting 1–4 Myr, has been variously described as unusual, strange, or out of equilibrium, as it has been argued that ecosystems function differently from those before and long after the extinction event, with strong biogeosphere feedbacks eventually leading to geologically stable ecosystems (Hull, 2015).

The early Cambrian [~ 541 – 509 million years ago (Ma)], Ordovician (~ 485 – 445 Ma), and mid-Triassic (~ 247 – 205 Ma) radiations were each associated with intervals of prolonged carbon cycle instability and biogeochemical cycle disruption (>1 Myr) preceded by widespread shallow marine anoxia – oceanic anoxic events (Fig. 1A). Here we propose that such episodes created evolutionary novelty and innovation. We apply specific definitions for these (Erwin, 2015), where ‘novelty’ is the establishment of new individuated phenotypic characters, for example the turtle carapace, feathers, or differentiated arthropod appendages (Wagner, 2014). Once novelties form these characters often diversify into many alternative character states (such as the variety of bird feathers), but these character states do not represent novelties. This is a very restrictive definition of novelty, but has the advantage of being relatively unambiguous and provides a conservative estimate of novelty in the cases considered here. By contrast, ‘innovation’ involves the transformation of ecological networks by the addition of new nodes, such that removal of these nodes from the network would result in measurable changes in structure using standard network analysis techniques. Innovation may be a prelude to phases of ‘diversification’ – that is the generation of new taxa, which may or may not increase morphological disparity (Erwin, 2015). Novelties may not necessarily lead directly to the establishment of a major new clade, or to ecological or evolutionary impact; there may often be a macroevolutionary lag between novelty and innovation (Erwin, 2015). Although many have assumed that novelty, innovation and diversification are linked, as in adaptive radiations, instances of macroevolutionary lags in fact demonstrate frequent decoupling (Erwin, 2015). Indeed, earlier studies found evidence for onshore origination of new orders that subsequently diversify into progressively offshore habitats (Jablonski *et al.*, 1983; Sepkoski & Miller, 1985; Jablonski & Bottjer, 1991). Post-Palaeozoic ordinal originations are associated, however, with frequent anoxic events (Jacobs & Lindberg, 1998) and may not be indicative of the origins of the morphological novelties associated with specific orders.

Below, we first consider the ecological dynamics of modern marine biota in fluctuating, dysoxic habitats and oxygen minimum zones, and how these processes might promote evolutionary novelty during intervals of prolonged anoxia. We then document ‘cryptic’ metazoan radiations during intervals of prolonged oceanic anoxia in the late Neoproterozoic–Cambrian, Cambro-Ordovician, and late

Permian–early Triassic that led to major radiations of skeletal biota.

II. LOW-OXYGEN HABITATS: ECOLOGY AND EVOLUTION

(1) Ecological dynamics of modern oxygen minimum zones

Critical oxygen thresholds with respect to animal function, ecology, and, hence evolution occur at low oxygen partial pressure (pO_2) levels (Sperling, Knoll & Girguis, 2015). Oxygen minimum zones (OMZs) are generally defined where O_2 levels are <0.5 ml/L, are stable over geological timescales (Levin, 2003), and have distinctive ecological features (Fig. 1B). Metazoans require oxygen, but thresholds vary markedly in relation to size, metabolism, mobility, and the presence or absence of an oxygen circulatory system (Vaquer-Sunyer & Duarte, 2008; Mills *et al.*, 2014). In modern marine environments, benthic diversity and biomass decreases with bottom-water O_2 levels, as does individual size, and the abundance of skeletal macrobenthos and predators (Rhodes & Morse, 1971). Although modern soft-bodied sponge-grade animals may tolerate O_2 concentrations as low as 1.25–10 mM (approximately 0.05–0.35 ml/L; Mills *et al.*, 2014), skeletonization is hypothesized to require higher O_2 levels, > 13 mM (approximately 0.4 ml/L; Levin *et al.*, 2000), in part because it requires synthesis of amino acids for collagen formation (Towe, 1970). The absence of biomineralization may also be related to reduced pH and carbonate saturation state, potentially increased pCO_2 , the higher energetic requirements of calcification under hypoxic conditions, or lower predation pressure (Sperling *et al.*, 2013).

Pelagic–benthic coupling is also reduced at low O_2 concentrations as are other measures of ecological complexity such as community succession: large individuals and long-lived equilibrium species are eliminated, and populations shift towards smaller short-lived species that often possess opportunistic life histories (Diaz & Rosenberg, 1995; Heim *et al.*, 2015). Core OMZs (<0.1 ml/L) are characterised by protistan and metazoan meiofauna (body sizes between 50 and 300 μm) which are probably favoured by their high tolerance to hypoxia combined with an abundant food supply and release from predation. Dominant metazoans are nematodes, oligochaetes, and polychaetes with thin body plans, enhanced respiratory surface areas and high-oxygen-affinity respiratory proteins (Thompson *et al.*, 1985; Levin *et al.*, 1997; Levin, 2003). At slightly higher O_2 levels (0.1–0.2 ml/L), deposit feeders and detritivores dominate, but food webs still remain relatively short (Sperling *et al.*, 2013). Macrofauna and megafauna often exhibit dense aggregations at OMZ edges, where O_2 is ~ 0.3 – 0.5 ml/L (Levin, 2003). When O_2 levels reach 0.5 ml/L ($\sim 8\%$ of modern surface ocean levels), the O_2 effects on macrofaunal carnivory and biodiversity become less pronounced (Sperling

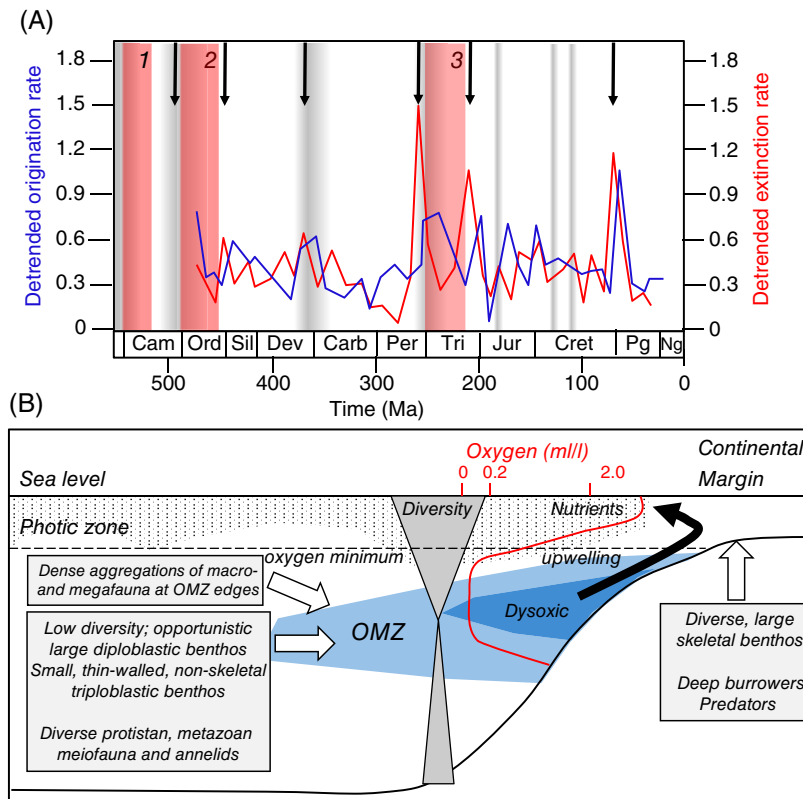


Fig. 1. (A) Phanerozoic origination rates (blue lines) and extinction rates (red lines) of marine invertebrate genera after detrending using exponential functions; data binned into 48 intervals averaging 11.0 Myr in duration (Alroy, 2008). Major mass extinctions (arrows), intervals of prolonged shallow marine anoxia (grey shading) and major radiation events (red shading) in the (i) Cambrian, (ii) Ordovician, and (iii) Triassic. Cam = Cambrian; Ord = Ordovician; Sil = Silurian; Dev = Devonian; Carb = Carboniferous; Perm = Permian; Tri = Triassic; Jur = Jurassic; Cret = Cretaceous; Pg = Paleogene; Ng = Neogene. (B) Ecological features of a modern oxygen minimum zone (OMZ) in relation to O₂ levels. Red line and scale shows approximate O₂ levels in ml/L (Rhodes & Morse, 1971; Levin, 2003; Vaquer-Sunyer & Duarte, 2008).

et al., 2013). Periods of prolonged ocean anoxia therefore create critical thresholds for the evolution of life, but not all these thresholds are equal.

Metazoans can be secondarily adapted to low O₂ conditions. For example, it has been proposed that some loriciferans spend their entire life cycle under anoxic conditions, relying upon hydrogenosome-like organelles associated with endosymbiotic prokaryotes rather than on true mitochondria (Danovaro *et al.*, 2010). Mitochondria themselves are highly plastic organelles that can be switched to operate anaerobically under both hypoxic conditions and in sea water with high sulphide concentrations (Doeller, Grieshaber & Kraus, 2001). Priapulid worms may also tolerate dysoxic conditions and are known to burrow within anaerobic substrates (Van der Land, 1970).

Ecological recovery from unstable redox is often rapid (<2 years) (Diaz & Rosenberg, 1995). A substantial part of the zooplankton lies dormant as eggs in the anoxic sediments which can be activated once sediments become oxic (Broman *et al.*, 2015), increasing benthic–pelagic coupling. Restoration of more stable or extensive oxic conditions promotes an increase in body size and growth rate, the re-appearance of

predation and skeletonization (Levin & Dayton, 2009) and an increase in rates of dispersal and benthic colonization (Santos & Simon, 1980; Levin *et al.*, 2009, *b*).

(2) A model for evolutionary dynamics during intervals of prolonged anoxia

As OMZs expand and contract over geological time they can influence evolutionary dynamics in a variety of ways. OMZs may affect genetic diversity and influence the speciation rate and alter the location of species in the ocean (White, 1987; Jacobs & Lindberg, 1998; Rogers, 2000). They may also (i) create strong gradients in O₂ over relatively short distances, and (ii) form barriers that block gene flow or reduce larval dispersal and migration, thereby isolating populations and promoting speciation (White, 1987; Jacobs & Lindberg, 1998; Rogers, 2000). Speciation alone may be insufficient to generate evolutionary novelties (Wagner, 2014; Erwin, 2015), but as we describe in the case studies below, OMZs may produce morphological novelties and generate the formation of new clades.

Animals in past low-O₂ or dominantly anoxic settings would almost certainly have been limited to non-skeletal,

small body sizes, low metabolic rates, low-energy feeding strategies and opportunistic lifestyles (Knoll & Sperling, 2014). Both Neoproterozoic and early Triassic ferruginous (rather than euxinic) oceans would have favoured the adoption of high-surface-area respiratory structures and body plans with reduced pressure from synergistic sulphide stress compared to modern metazoans. This has led to suggestions that such ferruginous, low-O₂ environments may have been more habitable to animals than modern oceans (Sperling *et al.*, 2016). Other models, however, show that even relatively modest levels of Fe²⁺ can significantly depress seasonal minima and maxima in dissolved O₂, thus creating metabolic effects that may have inhibited the emergence of metazoans for most of the Proterozoic (Reinhard *et al.*, 2016).

Mass extinctions are often associated with periods of prolonged anoxia (Fig. 1A) as well as global warming. The decimation of the skeletal benthos often removes ecological incumbents (Zhuravlev & Wood, 2009). Data show that oxic refuges were nonetheless available during subsequent ‘recovery’ intervals of prolonged anoxia, and both benthos and plankton rapidly colonize these settings (Hull, Darroch & Erwin, 2015; Clarkson *et al.*, 2016). Lilliput effects are also documented after many mass extinctions, representing temporary but significant reductions in body size of surviving taxa, which end following the return of oxic conditions (Urbanek, 1993; Twitchett, 2007; Wade & Twitchett, 2009).

Repatterning of gene regulatory networks (GRNs) is at the core of evolutionary novelty (Davidson & Erwin, 2010). Reduction in body size allows streamlining of developmental processes, producing flatter GRN hierarchies that may be more permissive of developmental repatterning. Such evolutionary changes may include novelty as well as the generation of new character states associated with existing attributes. In addition, adaptive refinement will generally be required to incorporate novel morphologies (Erwin, 2015).

Key morphological, functional, and ecological thresholds occur at O₂ levels below ~0.5 ml/L (Rhodes & Morse, 1971; Sperling *et al.*, 2015). Thus we propose a three-phase model of the association between anoxia and the origin and spread of morphological novelties consisting of a phase of innovation (recovery), and two phases of radiation intervals (Fig. 2). During the innovation phase, we suggest that small, soft-bodied biota acquired morphological novelties in variably oxic and dynamic settings and that this record would remain cryptic, i.e. not represented in the fossil record, but can be inferred from molecular phylogenies and molecular clock analyses (Phase 1: Fig. 2). We predict that the acquisition of skeletons, increases in body size and possibly increased life span will follow as O₂ levels increase or stabilize, during the subsequent radiation intervals. This will lead to the appearance of new, skeletal clades in the fossil record as well as increases in ecological complexity (Phase 2: Fig. 2). Thus maximum increases in disparity will be associated with Phase 2. Finally, taxic diversification and the generation of new character states will occur following stabilization of O₂ levels (Phase 3: Fig. 2). Phases 2 and 3 may overlap.

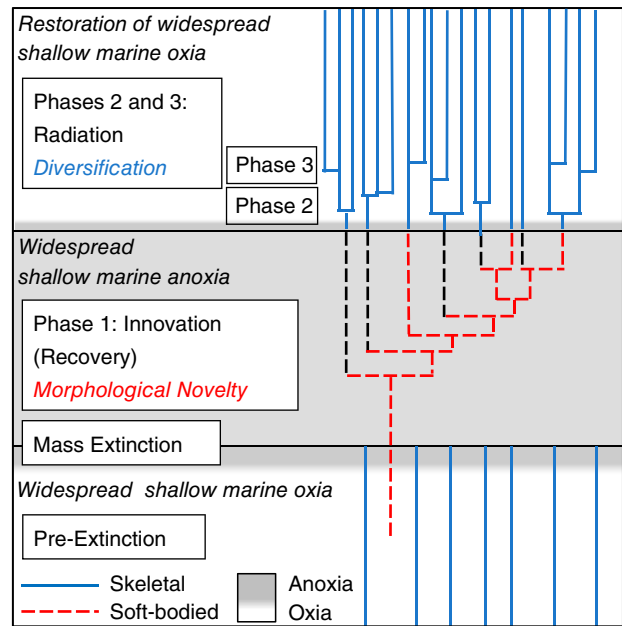


Fig. 2. Model for marine metazoan radiations in the context of oceanic redox evolution, divided into pre-extinction, mass extinction, innovation (recovery), and radiation intervals. Skeletal benthos incumbents are removed during mass extinctions, and high levels of morphological novelty in the small, soft-bodied benthos occur during the innovation (recovery) interval (Phase 1). The innovation (recovery) record remains mainly cryptic, inferred from molecular phylogenies and molecular clock analyses. Skeletal benthos radiates once widespread oxic conditions have been restored in the earliest radiation interval (Phase 2). Taxic diversification and the generation of new character states will occur following stabilization of O₂ levels in the later radiation interval (Phase 3).

III. ANOXIA AND RADIATIONS

Below we interrogate three intervals of major metazoan radiation to test the proposed three-phase model for the association between anoxia and the origin and spread of morphological novelties.

(1) Ediacaran anoxia and the Cambrian radiation

Both molecular clock studies (Erwin *et al.*, 2011) and the morphological, phylogenetic and biogeographic extent of the earliest Cambrian clades suggest a missing Neoproterozoic history of animals (Fig. 3A), although the two approaches differ regarding the length of this interval. Clades that appear in the Ediacaran and Cambrian radiation bear skeletons but can be inferred to have developed from soft-bodied ancestors (Valentine & Erwin, 1987; Wood, Ivantsov & Zhuravlev, 2017). Many key developmental novelties must also have preceded the late Neoproterozoic emergence of basal metazoan clades, including a gut, heart and central nervous system as well as clade-specific novelties (Tweedt & Erwin, 2015). The Cambrian radiation itself is associated

with increases in body size across many animal clades, skeletonization and the expansion of ecological networks (Erwin & Valentine, 2013), building from novelties that arose during the Ediacaran. Indeed, the first stages of metazoan evolution may have involved very small taxa in meiofaunal habitats, supporting a ‘cryptic’ history and explaining the discrepancy between the known fossil record of early metazoans and their estimated times of divergence based on molecular clocks.

Early Ediacaran oceans probably retained a Proterozoic-style, redox-stratified character, but the late Ediacaran represents an interval of extreme carbon cycle perturbation (Lyons *et al.*, 2014) (Fig. 3B). The Shuram–Wonoka excursion, occurring sometime between ~630 and ~551 Ma, represents a uniquely extreme negative $\delta^{13}\text{C}$ excursion, which has been suggested to represent the response to a major increase in atmospheric O_2 via oxidation of buried organic carbon. Although this is a primary and global signature, it has consistently defied explanation using conventional mass balance approaches (Grotzinger, Fike & Fischer, 2011). Geochemical studies have revealed a regionally heterogeneous redox landscape in Ediacaran oceans, with ferruginous anoxic conditions and intermittently shallow oxic waters on productive ocean margins and oxygenation, at least episodically, in deeper waters (Lyons *et al.*, 2014; Sperling *et al.*, 2015) (Fig. 3C). There is some evidence for extensive ocean oxygenation *ca.* 560–551 Ma (Kendall *et al.*, 2015), and possible multiple but transient episodes of widespread ocean oxygenation (‘oxic events’) towards the Ediacaran–Cambrian transition (Sahoo *et al.*, 2016). Indeed, models confirm that large spatiotemporal variations in surface ocean O_2 levels and pervasive benthic anoxia would be the result of much lower atmospheric $p\text{O}_2$ (Reinhard *et al.*, 2016). Productive shallow marine settings where most Ediacaran metazoan biodiversity is found show a patchy distribution of soft-bodied and skeletal metazoan communities that track oxic refugia (Wood *et al.*, 2015; Cui *et al.*, 2016a, 2016b), and were restricted to well-oxygenated waters [probably >10 mM (approximately 0.35 ml/l)] (Tostevin *et al.*, 2016).

These conditions persisted, at least regionally, into the early Cambrian (Canfield, Poulton & Narbonne, 2007; Jin *et al.*, 2016; Pages *et al.*, 2016) as episodic photic-zone euxinia is documented up to Cambrian Stage 3 or 4 (Canfield *et al.*, 2007; Pages *et al.*, 2016; Xiang *et al.*, 2017). This does not support the contention that stable levels of oxygenation were reached in the early Cambrian so promoting the radiation of bilaterians (Sperling *et al.*, 2013).

It is possible that the entire Cambrian radiation occurred under at least fluctuating anoxic conditions. However, thresholds of O_2 stability created by rising O_2 levels as well as rising concentrations of nutrients and calcium in shallow marine seas from the late Ediacaran to Cambrian (Brennan, Lowenstein & Horita, 2004) may have lowered seawater Mg/Ca, so promoting calcium carbonate precipitation in shallow waters. This would have enabled the radiation of larger individuals, and a more heavily skeletonized biota, in turn possessing more-sophisticated biomineralization mechanisms, in the early Cambrian, in part *via* ecological

feedbacks and predation-driven arms races. Interestingly, the potentially low- O_2 -tolerant loriciferans and priapulids, which belong to the cycloneuralians, comprise a significant part of early Cambrian diversity as well as biomass as shown by the large numbers of individuals present in soft-bodied communities. In addition, there is a notable increase in motile biota, including predators, relative to sessile attached and unattached biota during the Cambrian (Wood & Zhuravlev, 2012), as well as an overall increase in mean individual size during the Cambrian–Ordovician (Heim *et al.*, 2015).

Consistent with our model, most developmental and morphological innovations associated with the bilaterian body plans that appeared in the Cambrian must have occurred during the interval of low O_2 /unstable redox during the Ediacaran (Phase 1: Fig. 3). The widespread acquisition of skeletons, increases in body size, and radiation associated with the formation of new ecosystems appeared during the early stages of the Cambrian as habitable shallow marine environments become more widespread, possibly driven by an increase in O_2 levels leading to stabilization (Phase 2). Taxic diversification and the generation of new character states followed shortly thereafter (Phase 3).

(2) Late Cambrian anoxia and the Ordovician radiation

A second major phase of morphological novelty and innovation involved both plankton and animals during a series of complex, diachronous episodes known as the Ordovician radiation (Miller, 1997b; Webby *et al.*, 2004) (Fig. 4A). This sustained increase in taxonomic diversity of marine invertebrates (Alroy, 2008; Servais *et al.*, 2010) also included the first appearance of numerous classes and orders, including the earliest record of bryozoans (Ma *et al.*, 2015). The Ordovician radiation established the dominant Palaeozoic ecosystem structure, with substantial epifaunal and infaunal tiering, ecospace partitioning and complex ecological networks (Miller & Foote, 1996; Bambach, Bush & Erwin, 2007; Servais *et al.*, 2016).

This diversification began, however, in the late Cambrian, with a Furongian (Paibian to ‘Stage 10’) increase in plankton diversity evident in the appearance of a significant number of new morphologies of organic-walled microfossils (acritarchs), including dinoflagellate-like taxa (Nowak *et al.*, 2015; Servais *et al.*, 2016). Many bilaterian crown groups appeared in the late Cambrian, including annelids (Parry *et al.*, 2014), and both cephalopod (Mutvei, Zhang & Dunca, 2007) and gastropod molluscs. Associated changes included the independent development of a feeding, planktotrophic larval stage in diverse lineages, presumably in response to more abundant food resources and predation pressures from expanding epifaunal suspension feeders (Peterson & Butterfield, 2005). Rarefaction analysis of global diversity data established that much of this increase occurred during the Early Ordovician, peaking near the base of the Middle Ordovician (Miller & Foote, 1996; Droser & Finnegan, 2003), in contrast to raw diversity records that suggest a continued increase in generic diversity through the Ordovician.

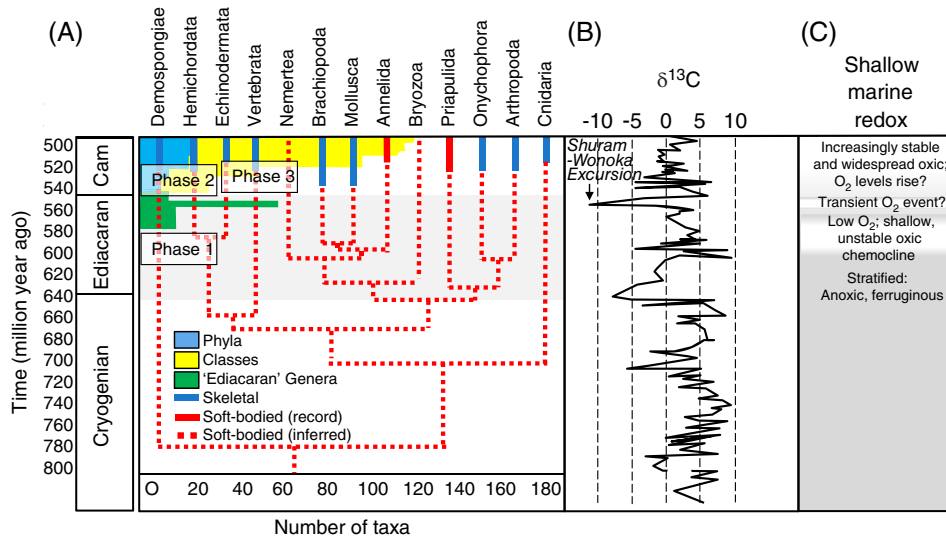


Fig. 3. Neoproterozoic–Cambrian metazoan radiation and environmental context. (A) Molecular timescale and fossil record of animal evolution, with appearance of animal phyla and classes in the fossil record (Erwin *et al.*, 2011) and inferred timing of metazoan radiation Phases 1, 2 and 3 (see Fig. 2). Number of taxa given as block shading behind cladogram, with Ediacaran genera (green), and Cambrian phyla (blue) and classes (yellow). (B) $\delta^{13}\text{C}$ record (Erwin *et al.*, 2011). (C) Generalized record of shallow marine redox (Lyons, Reinhard & Planavsky, 2014; Kendall *et al.*, 2015; Sahoo *et al.*, 2016). Cam = Cambrian.

The globally recognized Upper Cambrian large positive $\delta^{13}\text{C}$ Steptoean positive carbon isotope excursion (SPICE) is a major perturbation in the global carbon cycle (Fig. 4B). The SPICE shows a shift of approximately 4‰, and is also associated with an approximately 20‰ increase in the $^{34}\text{S}/^{32}\text{S}$ ratio of sea water as measured in carbonate-associated sulphate (Saltzman *et al.*, 2011). This is interpreted to represent an interval of several million years of enhanced organic carbon and pyrite sulphur levels beneath anoxic (euxinic) waters (Saltzman *et al.*, 2011). Oxygen deficiency may have been widespread below the surface mixed layer of late Cambrian oceans, such that upwelling of anoxic waters during sea-level rise may have been a primary cause of the global extinction at the base of the Paibian Stage (Gill *et al.*, 2011). There may be a link between other $\delta^{13}\text{C}$ excursions, extinctions and anoxic events that persisted into the Early Ordovician, such as during the Upper Tremadocian (Saltzman *et al.*, 2015). Sea-level rise may have brought anoxic waters onto the shelf to initiate extinctions. Evidence for $\delta^{13}\text{C}$ excursions and elevated extinction rates appears to wane in the late Tremadocian. This is consistent with progressive oxygenation of the oceans reaching a threshold that helped facilitate initial stages of the Great Ordovician Biodiversification Event (Saltzman *et al.*, 2015). Th/U ratios indicate that increases in marine O_2 levels may have begun in the earliest Ordovician (Marengo *et al.*, 2016).

Indeed, the entire late early Cambrian to late Cambrian interval shows a number of faunal extinctions and recoveries, first described as ‘biomere events’ in western North America (Palmer, 1965) but later shown to be of global significance (Zhuravlev, 2001). Furthermore, the late Cambrian to Middle Ordovician records a plateau in animal diversity that was maintained by repeated extinction and recovery

(Bambach, Knoll & Wang, 2004). The SPICE event coincides with one such biomere, and others coincide with more minor C-isotope excursions that may reflect general redox instability of the ocean. Most of the associated morphological novelties arose during the latest Cambrian or early Ordovician may be coincident with major carbon-cycle perturbations, some of which involved periods of anoxia, perhaps due to sea-level driven upwelling (Saltzman *et al.*, 2015), followed by an increase in atmospheric oxygenation. The expansion of the zooplankton represented a critical initial step in the expansion of ecological networks (Tweedt & Erwin, 2015; Servais *et al.*, 2016) that allowed animal groups to increase in size and spread into increasingly oxygenated and ecologically diverse marine habitats, so establishing the complex ecosystems that are a hallmark of the Ordovician Radiation (Phase 1; Fig. 4). This was followed by a progressive expansion of taxonomic diversity and ecological complexity in the Early to Middle Ordovician (Phases 2 and 3). This is consistent with the model proposed here. Unresolved, however, is whether a simple rise in oxygenation was the major control on taxonomic diversification during this interval, or whether the key factor was the spatial heterogeneity produced by isolation of multiple shallow-water basins by anoxic barriers. The well-known spatial and temporal complexity of this event (Miller, 1997*a,b*; Droser & Finnegan, 2003; Trubovitz & Stigall, 2016) therefore provides an opportunity to test our hypothesis further by considering differences in local responses.

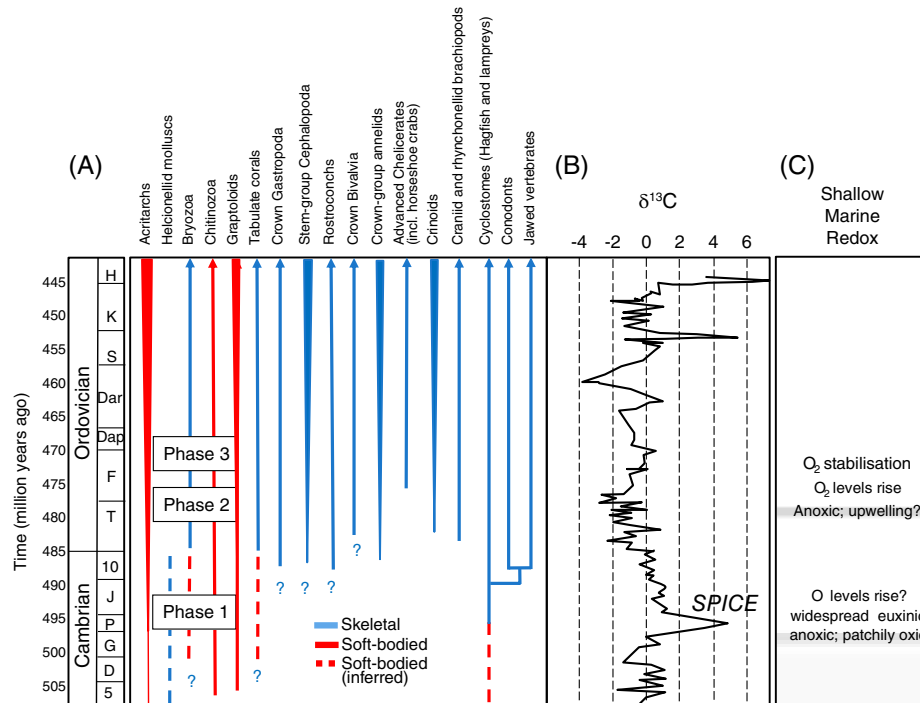


Fig. 4. Late Cambrian–Ordovician radiation and environmental context. (A) Generalized fossil record of marine invertebrates (Donoghue, Forey & Aldridge, 2000; Webby *et al.*, 2004; Kröger, Vinther & Fuchs, 2011; Shen *et al.*, 2013; Parry, Tanner & Vinther, 2014; Ma *et al.*, 2015; Vinther, 2015; Carlson, 2016; Servais *et al.*, 2016) with inferred timing of metazoan radiation Phases 1, 2 and 3 (see Fig. 2). (B) $\delta^{13}\text{C}$ record showing Steptoean positive carbon isotope excursion (SPICE) event (Gradstein *et al.*, 2012). (C) Generalized record of shallow marine redox (Saltzman *et al.*, 2011, 2015; Marengo *et al.*, 2016). Cambrian stages: 5 = ‘Stage 5’; D = Drumian; G = Guzhangian; P = Paibian; J = Jiangshangian; 10 = ‘Stage 10’. Ordovician stages: T = Tremadocian; F = Floian; Dap = Dapingian; Dar = Darriwilian; S = Sandbian; K = Katian; H = Hirnantian.

(3) Permo-Triassic extinction and Triassic radiation

The end-Permian mass extinction (251.8 Ma) was the most severe of the Phanerozoic, with estimates that 68% of genera and up to 92% of species did not survive into the Triassic (Erwin, 2006) (Fig. 5A). The pattern of extinction is highly differential, with epifaunal suspension-feeding clades heavily affected. Ecosystems collapsed, leading to a pervasive change in the composition and structure of marine ecosystems. Although the environmental changes during the extinction interval are complex, a consensus has emerged that Siberian trap volcanism caused the extinction *via* $p\text{CO}_2$ changes and possibly CH_4 influx, leading to hypoxia, global warming, ocean acidification, and the expansion of anoxia in OMZs (Knoll *et al.*, 2007; Burgess, Bowring & Shen, 2014; Burgess & Bowring, 2015; Burgess, Muirhead & Bowring, 2017).

In the aftermath of the extinction a distinctive record of sedimentary and geochemical features reveal a highly protracted ‘recovery’ interval that lasted some 4–5 Myr (Payne *et al.*, 2004; Knoll *et al.*, 2007). The pronounced negative excursion of $\delta^{13}\text{C}$ recorded during the end-Permian extinction (Shen, Shen & Crowley, 2011), with continuing excursions throughout the Early Triassic (Payne *et al.*, 2004) (Fig. 5B) are associated with continued but highly

dynamic anoxia, ferruginous in the Neo-Tethys (Clarkson *et al.*, 2016) but possibly euxinic in the Tethys (Grasby *et al.*, 2013) (Fig. 5C). The Arabian margin, for example, records repeated expansion of ferruginous conditions where the maximum extent of anoxia is consistently associated with globally recorded positive $\delta^{13}\text{C}$ excursions at both the Induan/Olenekian boundary (shallow-water anoxia) and the ‘Smithian/Spathian’ (mid-Olenekian) boundary (mid-slope anoxia) (Clarkson *et al.*, 2016). Unusual seafloor carbonate precipitates appear episodically throughout this interval, suggesting elevated alkalinity (Fig. 5A). The extent of anoxia was probably aided by the elevation of temperatures by 6–10°C in the Olenekian (Sun *et al.*, 2012; Chen *et al.*, 2016). Shallow-water oxia was therefore highly restricted but when periods of regionally stable but short-lived oxygenation occurred, they facilitated rapid biotic recovery (Clarkson *et al.*, 2016).

The anoxia associated with the extinction and post-extinction interval is reflected in differential extinction and recovery. An analysis of extinction pattern identifies differential extinction of heavily calcified groups with passive respiratory systems, which were unable to buffer against decreasing $[\text{CO}_3^{2-}]$. In a world of rapid increase in $p\text{CO}_2$, hypercapnia (CO_2 poisoning) would result (Knoll *et al.*, 1996). Hypercapnia would preferentially affect calcified sponges

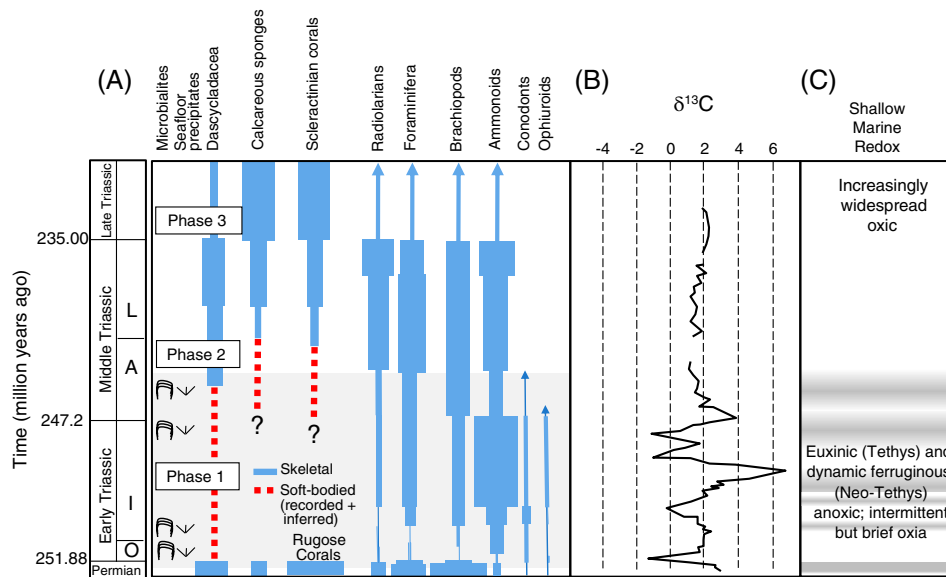


Fig. 5. Late Permian–Triassic radiation and environmental context. (A) Record of marine microbialites, carbonate sea-floor precipitates, invertebrates, algae and protists (Erwin, 2006; Chen & Benton, 2012) with inferred timing of metazoan radiation Phases 1, 2 and 3 (see Fig. 2). (B) $\delta^{13}\text{C}$ record (Payne *et al.*, 2004). (C) Generalized record of shallow marine redox (Grasby *et al.*, 2013; Clarkson *et al.*, 2016). Triassic stages: O = Olenekian; I = Induan; A = Anisian; L = Ladinian.

and corals, and calcareous green and red algae, rhyzonelliform brachiopods, crinoids, and bryozoans – the major reef-builders and carbonate-sediment producers of the Palaeozoic – as well as other groups. A global decline in body size at the Permo-Triassic boundary, and continuing into the early Triassic, has been documented for gastropods, bivalves, calcitic and phosphatic brachiopods, ostracods, conodonts, and foraminiferans; only ammonoids show an increase in size (Schaal *et al.*, 2016). Low- O_2 -tolerant species are selectively seen in the Early Triassic fossil record (Twitchett *et al.*, 2004; Erwin, 2006). Stabilization of the $\delta^{13}\text{C}$ signal occurred by the Anisian (middle Triassic), coincident with the loss of unusual sedimentological features, the oxygenation of shallow marine platforms, and the widespread resumption of ‘normal’ shallow marine carbonate production, i.e. under dominantly biological control *via* calcareous biomineralization (Fig. 5A,B).

The pattern of recovery during the Early Triassic is highly uneven, both taxonomically and temporally. Early Triassic communities were dominated by mollusc and phosphatic brachiopods, with an increase in crinoid abundance in the Olenekian (Erwin, 2006). These are taxa with moderate skeletal mass whose skeletons formed from fluids that are relatively well buffered with respect to the factors that govern carbonate precipitation (Knoll *et al.*, 1996). Accelerated ecological recovery took place in the Olenekian to Anisian, but taxa without physiological buffering were absent from the Early Triassic record and did not appear until the Anisian.

Molecular and fossil evidence demonstrates that the anomalous high CO_2 levels and anoxic world of the Early Triassic represents a period of origination and diversification of the non-skeletal ancestors of many major Mesozoic skeletal groups (Phase 1; Fig. 5A). For example, although the origin

of the Scleractinian corallimorph clade is unclear, 20 species assigned to 7–9 suborders appear in the Anisian (Veron, 1995). All these groups have close living non-skeletal relatives which unlike their skeletal counterparts are not restricted to high-carbonate-saturation waters. Late Permian calcified sponges and corals, calcareous red algae and dasyclad green algae disappeared, but their unskeletonized relatives did not (Knoll *et al.*, 2007).

Skeletonization, progressive expansion of taxonomic diversity and ecological complexity followed in the Middle to Late Triassic (Phases 2 and 3). Several groups of marine reptiles also appear in the early Triassic, including ichthyosauromorphs, sauropterygians, and thalattosaurs (Kelley & Pyenson, 2015), with novelties in each clade. Phylogenetic analysis shows that ichthyosaurs had undergone extensive taxonomic and morphological innovation within the first million years of the Triassic (Jiang *et al.*, 2016). Additionally, numerous crown-neopterygian fish appear during this interval (Friedman, 2015).

The unusual epiphenomena of the late Permian to Early Triassic are directly related to the anomalously high and rapid increase of $p\text{CO}_2$ from volcanic activity, leading to global temperature elevation and hence unstable and dynamic anoxia in the shallow marine realm. This is expressed both as unusual seafloor carbonate precipitates as well as various physiological responses leading to the selective extinction of poorly buffered skeletal taxa, a reduction in individual body size, and changes in benthic community composition. Whilst the extrinsic controls on the creation of shallow marine anoxia might differ from the Neoproterozoic–Cambrian and Cambrian–Ordovician, we argue that the general evolutionary response to these events

was similar: protracted anoxia leading to the origination and diversification of non-skeletal biota that were the ancestors of future, major skeletal groups.

IV. CONCLUSIONS

(1) Morphological novelties and innovations were widespread during the Ediacaran–Cambrian, late Cambrian–Ordovician and Early Triassic radiations. Indeed, suggestions that ecological opportunities were generated during each interval have been discussed widely for decades. Here, we argue that oceanic anoxia associated with these events created the environmental conditions favourable for the generation of morphological novelties, and that these in turn led to evolutionary innovation and taxonomic diversification as environmental conditions ameliorated.

(2) While the importance of low O_2 levels is a common thread between the three radiations, the role of O_2 during the Ediacaran–Cambrian radiation may be a complex manifestation of the shallow marine realm first reaching a critical O_2 threshold to support complex metazoans and the evolution of skeletons. The subsequent late Cambrian–Ordovician and Early Triassic radiations were created by the removal of skeletal benthic incumbents by mass-extinction events, and the succeeding intervals of dominantly anoxic seas that promoted the evolution of morphological novelty.

(3) Each of the three radiation events considered here is associated with the establishment of major animal clades. In classic Linnean terms, phyla first appear near the Ediacaran–Cambrian boundary due to an increase in size; the Ordovician diversification is associated with the appearance of many invertebrate classes and orders (metazoan crown groups), and many new orders of vertebrates and invertebrates first appear during the Triassic recovery. Thus, the overwhelming majority of metazoan clades and their accompanying novelties are associated with these three episodes.

(4) The terms novelty and innovation are used in many different ways, often interchangeably (Moczek, 2008; Brigandt & Love, 2012; Erwin, 2015), but here we use specific definitions (Erwin, 2015): novelty applies to the origin of newly individuated morphological characters; innovation is recognized by the restructuring of ecological networks such that the removal of the new node(s) would trigger collapse of the network; and taxonomic diversification is the generation of new taxa, not necessarily associated with either novelty or innovation.

(5) In the cases described here, we show that the establishment of new clades, with their attendant morphological novelties, must have been preceded by phases of cryptic diversification of soft-bodied metazoans. These phases of cryptic diversification occurred during intervals of major carbon-cycle perturbation and dynamic oceanic redox conditions which were nevertheless dominated by widespread anoxia. Previous workers have suggested that

new taxa preferentially arise in near nearshore habitats. By contrast we suggest that morphological novelties may in fact be generated under anoxic conditions (whether offshore or nearshore). Widespread skeletonization, innovations and taxonomic diversification occurred as conditions improved, which may have initially occurred in warm, shallow, oxic (i.e. nearshore) habitats.

(6) We conclude that anoxic intervals should no longer be regarded as unfavourable, but on the contrary, they should be considered as providing the environmental conditions for notable generation of novelty on evolutionary timescales.

(7) Intervals following mass extinctions do not represent ‘recovery’, but rather create critical thresholds for the appearance of evolutionary novelty, innovation, and diversification. As a result, we propose that so-called ‘recovery’ intervals after mass extinctions might better be considered as ‘innovation’ intervals.

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VI. REFERENCES

- ALROY, J. (2008). Dynamics of origination and extinction in the marine fossil record. *Proceedings of the National Academy of Science* **105**, 11536–11542.
- BAMBACH, R. K., BUSH, A. M. & ERWIN, D. H. (2007). Autecology and the filling of ecospace: key metazoan radiations. *Palaeontology* **50**, 1–22.
- BAMBACH, R. K., KNOLL, A. H. & WANG, S. (2004). Origination, extinction, and mass depletions of marine diversity. *Paleobiology* **30**, 522–542.
- BOYLE, R. A. & LENTON, T. M. (2006). Fluctuation in the physical environment as a mechanism for reinforcing evolutionary transitions. *Journal of Theoretical Biology* **242**, 832–843.
- BRENNAN, S. T., LOWENSTEIN, T. K. & HORITA, J. (2004). Seawater chemistry and the advent of biocalcification. *Geology* **32**, 473–476.
- BRIGANDT, I. & LOVE, A. C. (2012). Conceptualizing evolutionary novelty: moving beyond definitional debates. *Journal of Experimental Zoology B* **318B**, 417–427.
- BROMAN, E., BRUSIN, M., DOPSON, M. & HYLANDER, S. (2015). Oxygenation of anoxic sediments triggers hatching of zooplankton eggs. *Proceedings of the Royal Society B: Biological Science* **282**, 2015–2025.
- BURGESS, S. D. & BOWRING, S. A. (2015). High-precision geochronology confirms voluminous magmatism before, during, and after Earth’s most severe extinction. *Science Advances* **1**, e1500470.
- BURGESS, S. D., BOWRING, S. A. & SHEN, S. Z. (2014). A high-precision timeline for Earth’s most severe extinction. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 3316–3321.
- BURGESS, S. D., MUIRHEAD, J. D. & BOWRING, S. A. (2017). Initial pulse of Siberian traps sills as the trigger of the end-Permian mass extinction. *Nature Communications* **8**, 164.
- CANFIELD, D. E., POULTON, S. W. & NARBONNE, G. M. (2007). Late-Neoproterozoic deep-ocean oxygenation and the rise of animal life. *Science* **315**, 92–95.
- CARLSON, S. J. (2016). The evolution of Brachiopoda. *Annual Reviews of Earth and Planetary Sciences* **44**, 409–438.
- CHEN, J., SHEN, S. Z., LI, X.-H., XU, Y.-G., JOAMCHIMSKI, M. M., BOWRING, S. A., ERWIN, D. H. & YUAN, D. X. (2016). High-resolution SIMS oxygen isotope analysis on conodont apatite from South China and implications for the end-Permian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* **448**, 26–38.
- CHEN, Z. Q. & BENTON, M. J. (2012). The timing and pattern of biotic recovery following the end-Permian mass extinction. *Nature Geoscience* **5**, 375–383.
- CLARKSON, M. O., WOOD, R. A., POULTON, S. W., RICHOX, S., NEWTON, R. J., KASEMANN, S. A., BOWYER, F. & KRYSYTN, L. (2016). Dynamic anoxic

- ferruginous conditions during the end-Permian mass extinction and recovery. *Nature Communications* **7**, 12236.
- CUI, H., KAUFMAN, A. J., XIAO, S., PEEK, S., CAO, H., MIN, X., CAI, Y., SIEGEL, Z., LIU, X.-M., PENG, Y., SCHIFFBAUER, J. D. & MARTIN, A. J. (2016a). Environmental context for the terminal Ediacaran biomineralization of animals. *Geobiology* **12**, 178.
- CUI, H., GRAZHDANKIN, D. V., XIAO, S., PEEK, S., ROGOV, V. I., BYKOVA, N. V., SIEVERS, N. E., LIU, X.-M. & KAUFMAN, A. J. (2016b). Redox-dependent distribution of early macro-organisms: evidence from the terminal Ediacaran Khatyspyt formation in Arctic Siberia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **461**, 122–139.
- DANOVARO, R., DELL'ANNO, A., PUSCEDDU, A., GAMBI, C., HEINER, I. & KRISTENSEN, R. M. (2010). The first Metazoa living in permanently anoxic conditions. *BMC Biology* **8**, 30.
- DAVIDSON, E. H. & ERWIN, D. H. (2010). Evolutionary innovation and stability in animal gene networks. *Journal of Experimental Zoology* **314B**, 182–186.
- DIAZ, R. J. & ROSENBERG, R. (1995). Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology* **33**, 245–303.
- DOELLER, J. E., GRIESHABER, M. K. & KRAUS, D. W. (2001). Chemolithoheterotrophy in a metazoan tissue: thiosulfate production matches ATP demand in ciliated mussel gills. *Journal of Experimental Biology* **204**, 3755–3764.
- DONOGHUE, P. C., FOREY, P. L. & ALDRIDGE, R. J. (2000). Conodont affinity and chordate phylogeny. *Biological Reviews* **75**, 191–251.
- DROSER, M. L. & FINNEGAN, S. (2003). The Ordovician radiation: a follow-up to the Cambrian explosion? *Integrative and Comparative Biology* **43**, 178–184.
- ERWIN, D. H. (2006). *Extinction: How Life Nearly Died 250 Million Years Ago*. Princeton University Press Princeton, New Jersey.
- ERWIN, D. H. (2015). Novelty and Innovation in the History of Life. *Current Biology* **25**, R930–R940.
- ERWIN, D. H., LAFLAMME, M., TWEEDT, S. M., SPERLING, E. A., PISANI, D. & PETERSON, K. J. (2011). The Cambrian Conundrum: early divergence and later ecological success in the early history of animals. *Science* **334**, 1091–1097.
- ERWIN, D. H. & VALENTINE, J. W. (2013). *The Cambrian Explosion: The Construction of Animal Biodiversity*. Roberts & Co. Greenwood Village.
- FRIEDMAN, M. (2015). The early evolution of ray-finned fishes. *Palaeontology* **58**, 213–228.
- GILL, B. C., LYONS, T. W., YOUNG, S. A., KUMP, L. R., KNOLL, A. H. & SALTZMAN, M. R. (2011). Geochemical evidence for widespread euxinia in the later Cambrian ocean. *Nature* **469**, 80–83.
- GRADSTEIN, F. M., OGG, J. G., SCHMITZ, M. D. & OGG, G. M. (2012). *The Geologic Time Scale (Volume 1)*. Elsevier, Boston.
- GRASBY, S. E., BEAUCHAMP, B., EMBRY, A. & SANEI, H. (2013). Recurrent Early Triassic ocean anoxia. *Geology* **41**, 175–178.
- GROTZINGER, J. P., FIKE, D. A. & FISCHER, W. W. (2011). Enigmatic origin of the largest-known carbon isotope excursion in Earth's history. *Nature Geoscience* **4**, 285–292.
- HEIM, N. A., KNOPE, M. L., SCHAAL, E. K., WANG, S. C. & PAYNE, J. L. (2015). Cope's rule in the evolution of marine animals. *Science* **347**, 867–870.
- HULL, P. M. (2015). Life in the aftermath of mass extinction. *Current Biology* **25**, R941–R952.
- HULL, P. M., DARROCH, S. A. F. & ERWIN, D. H. (2015). Mass extinctions, rarity and the future of ecosystems. *Nature* **528**, 345–351.
- JABLONSKI, D. & BOTTJER, D. J. (1991). Environmental patterns in the origins of higher taxa: the post-Paleozoic fossil record. *Science* **252**, 1831–1833.
- JABLONSKI, D., SEPKOSKI, J. J., BOTTJER, D. J. & SHEEHAN, P. M. (1983). Onshore-Offshore Patterns in the Evolution of Phanerozoic Shelf Communities. *Science* **222**, 1123–1112.
- JACOBS, D. K. & LINDBERG, D. R. (1998). Oxygen and evolutionary patterns in the sea: onshore/offshore trends and recent recruitment of deep-sea faunas. *Proceedings of the National Academy of Sciences of the United States of America* **95**, 9396–9401.
- JIANG, D. Y., JIANG, D.-Y., MOTANI, R., HUANG, J.-D., TINTORI, A., HU, Y.-C., RIEPPEL, O., FRASER, N.-C., JI, C., KELLEY, N. P., FU, W. L. & ZHANG, R. (2016). A large aberrant stem ichthyosauriform indicating early rise and demise of ichthyosauromorphs in the wake of the end-Permian extinction. *Scientific Reports* **6**, 26232.
- JIN, C. S., LI, C., ALGEO, T. J., PLANAVSKY, N. J., CUI, H., YANG, X., ZHAO, Y., ZHANG, X. & XIE, S. (2016). A highly redox-heterogeneous ocean in south china during the early Cambrian (529–514 Ma): implications for biota-environment co-evolution. *Earth and Planetary Science Letters* **441**, 38–45.
- KELLEY, N. P. & PYENSON, N. D. (2015). Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene. *Science* **348**(6232), 3716–1–3716-7.
- KENDALL, B., KOMIYA, T., LYONS, T. W., BATES, S. M., GORDON, G. W., ROMANIELLO, S. G., JIANG, G., CREASER, R. G., XIAO, S., MCFADDEN, K., SAWAKI, Y., TAHATA, M., SHU, D., HAN, J., LI, Y., CHU, X. & ANBAR, A. D. (2015). Uranium and molybdenum isotope evidence for an episode of widespread ocean oxygenation during the late Ediacaran Period. *Geochimica et Cosmochimica Acta* **156**, 173–193.
- KNOLL, A. H., BAMBACH, R. K., CANFIELD, D. E. & GROTZINGER, J. P. (1996). Comparative earth history and late Permian mass extinction. *Science* **273**, 452–457.
- KNOLL, A. H., BAMBACH, R. K., PAYNE, J. L., PRUSS, S. B. & FISCHER, W. W. (2007). Paleophysiology and end-Permian mass extinction. *Earth and Planetary Science Letters* **256**, 295–313.
- KNOLL, A. H. & SPERLING, E. A. (2014). Oxygen and animals in Earth history. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 3907–3908.
- KNOPE, M. L., HEIM, N. A., FRISHKOFF, L. O. & PAYNE, J. L. (2015). Limited role of functional differentiation in early diversification of animals. *Nature Communications* **6**, 6455.
- KRÖGER, B., VINTHER, J. & FUCHS, D. (2011). Cephalopod origin and evolution: a congruent picture emerging from fossils, development and molecules. *BioEssays* **33**, 602–613.
- KRUG, A. Z., JABLONSKI, D. & VALENTINE, J. W. (2009). Signature of the end-Cretaceous mass extinction in the modern biota. *Science* **323**, 767–771.
- LEVIN, L. A. (2003). Oxygen minimum zone benthos: adaptation and community response to hypoxia. *Oceanographic and Marine Biology* **41**, 1–45.
- LEVIN, L. A. & DAYTON, P. K. (2009). Ecological theory and continental margins: where shallow meets deep. *Trends in Ecology Evolution* **24**, 606–627.
- LEVIN, L. A., EKAU, W., GOODAY, A., JORRISEN, F., MIDDELBURG, J., NEIRA, C., RABALAIS, N., NAQVI, S. W. A. & ZHANG, J. (2009). Effects of natural and human-induced hypoxia on coastal benthos. *Biogeosciences* **6**, 2063V2098.
- LEVIN, L. A., GAGE, J. D., LAMONT, P., CAMMIDGE, L., MARTIN, C., PATIENCE, A. & CROOKS, J. (1997). Infaunal community structure in a low-oxygen, organic rich habitat on the Oman continental slope, NW Arabian Sea. In *Responses of Marine Organisms to their Environments. Proceedings of the 30th European Marine Biology Symposium* (eds L. HAWKINS and S. HUTCHINSON), pp. 223–230. Southampton, Southampton Oceanography Centre.
- LEVIN, L. A., GAGE, J. D., MARTIN, C. & LAMONT, P. A. (2000). Macrobenthic community structure within and beneath the oxygen minimum zone, NW Arabian Sea. *Deep-Sea Research* **47**, 189–226.
- LEVIN, L. A., MENDOZA, G. F., KONOTCHICK, T. & LEE, R. (2009). Community structure and trophic relationships in Pacific hydrothermal sediments. *Deep-Sea Research II* **56**, 1632–1648.
- LYONS, T. W., REINHARD, C. T. & PLANAVSKY, N. J. (2014). The rise of oxygen in Earth's early ocean and atmosphere. *Nature* **506**, 307–315.
- MA, J. Y., TAYLOR, P. D., XIA, F. S. & ZHAN, R. B. (2015). The oldest known bryozoan: *Prophyllodictya* (Cryptostomata) from the lower Tremadocian (Lower Ordovician) of Liujiachang, south-western Hubei, central China. *Palaeontology* **58**, 925–934.
- MARENCO, P. J., MARTIN, K. R., MARENCO, K. N. & BARBER, D. C. (2016). Increasing global ocean oxygenation and the Ordovician Radiation: insights from Th/U of carbonates from the Ordovician of western Utah. *Palaeogeography, Palaeoclimatology, Palaeoecology* **458**, 77–84.
- MILLER, A. I. (1997a). Comparative diversification dynamics among palaeocontinents during the Ordovician radiation. *Geobios* **20**, 397–406.
- MILLER, A. I. (1997b). Dissecting global diversity patterns: examples from the Ordovician radiation. *Annual Review of Ecology and Systematics* **28**, 85–104.
- MILLER, A. I. & FOOTE, M. (1996). Calibrating the Ordovician Radiation of marine life: implications for Phanerozoic diversity trends. *Paleobiology* **22**, 304–309.
- MILLS, D. B., WARD, L. M., JONES, C., SWEETEN, B., FORTH, M., TREUSCH, A. H. & CANFIELD, D. E. (2014). The oxygen requirements of sponges: modern analogues for the earliest animals. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 9073–9078.
- MOCZEK, A. P. (2008). On the origins of novelty in development and evolution. *BioEssays* **30**, 432–447.
- MUTVEI, H., ZHANG, Y.-B. & DUNCA, E. (2007). Late Cambrian Ectoproterid nautiloids and their role in cephalopod evolution. *Palaeontology* **50**, 1327–1333.
- NOWAK, H., SERVAIS, T., MONNET, C., MOLYNEUX, S. G. & VANDENBROUCKE, T. R. A. (2015). Phytoplankton dynamics from the Cambrian Explosion to the onset of the Great Ordovician Biodiversification Event: a review of Cambrian acritarch diversity. *Earth-Science Reviews* **151**, 117–131.
- PAGES, A., SCHMID, S., EDWARDS, D., BARNES, S., HE, N. & GRICE, K. (2016). A molecular and isotopic study of palaeoenvironmental conditions through the middle Cambrian in the Georgina Basin, central Australia. *Earth and Planetary Science Letters* **447**, 21–32.
- PALMER, A. R. (1965). Biome: a new kind of biostratigraphic unit. *Journal of Paleontology* **39**, 149–153.
- PARRY, L., TANNER, A. & VINTHER, J. (2014). The origin of annelids. *Palaeontology* **57**, 1091–1103.
- PAYNE, J. L., LEHRMANN, D. J., WEI, J., ORCHARD, M. J., SCHRAG, D. P. & KNOLL, A. H. (2004). Large perturbations of the carbon cycle during recovery from the end-Permian extinction. *Science* **305**, 506–509.
- PETERSON, K. J. & BUTTERFIELD, N. J. (2005). Origin of the Eumetazoa: testing ecological predictions of molecular clocks against the Proterozoic fossil record. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 9547–9552.

- REINHARD, C. T., PLANAVSKY, N. J., OLSON, S. L., LYONS, T. W. & ERWIN, D. H. (2016). Earth's oxygen cycle and the evolution of animal life. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 8933–8938.
- RHODES, D. C. & MORSE, J. W. (1971). Evolutionary and ecologic significance of oxygen-deficient marine basins. *Lethaia* **4**, 413–428.
- ROGERS, A. D. (2000). The role of the oceanic oxygen minima in generating biodiversity in the deep sea. *Deep-Sea Research* **47**, 119–148.
- SAHOO, S. K., PLANAVASKY, N. J., JIANG, G., KENDALL, B., OWENS, J. D., WANG, X., SHI, X., ANBAR, A. D. & LYONS, T. W. (2016). Oceanic oxygenation events in the anoxic Ediacaran ocean. *Geobiology* **14**, 457–468.
- SALTZMAN, M. R., EDWARDS, C. T., ADRAIN, J. M. & WESTROP, S. R. (2015). Persistent oceanic anoxia and elevated extinction rates separate the Cambrian and Ordovician radiations. *Geology* **43**, 807–810.
- SALTZMAN, M. R., YOUNG, S. A., KUMP, L. R., GILL, B. C., LYONS, T. W. & RUNNEGAR, B. (2011). Pulse of atmospheric oxygen during the late Cambrian. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 3876–3881.
- SANTOS, S. L. & SIMON, J. L. (1980). Response of soft-bottom benthos to annual catastrophic disturbance in a South Florida estuary. *Marine Ecology Progress Series* **3**, 347–355.
- SCHAAL, E. K., CLAPHAM, M. E., REGO, B. L., WANG, S. C. & PAYNE, J. L. (2016). Comparative size evolution of marine clades from the Late Permian through Middle Triassic. *Paleobiology* **42**, 127–142.
- SEPKOSKI, J. J. JR. & MILLER, A. I. (1985). Evolutionary marine faunas and the distribution of Paleozoic benthic communities in space and time. In *Phanerozoic Diversity Patterns* (ed. J. W. VALENTINE). Princeton University Press Princeton, New Jersey. 153–190.
- SERVAIS, T., OWEN, A. W., HARPER, D. A. T., KROGER, B. & MUNNECKE, A. (2010). The Great Ordovician Biodiversification Event (GOBE): the palaeoecological dimension. *Palaeogeography, Palaeoclimatology, Palaeoecology* **294**, 99–119.
- SERVAIS, T., SERVAIS, T., PERRIER, V., DANELIAN, T., KLUG, C., MARTIN, R., MUNNECKE, A., NOWAK, H., NÜTZEL, A., VANDENBROUCKE, T. R. A., WILLIAMS, M. & RASMUSSEN, C. M. Ø. (2016). The onset of the 'Ordovician Plankton Revolution' in the late Cambrian. *Palaeogeography, Palaeoclimatology, Palaeoecology* **458**, 12–28.
- SHEN, C., ALDRIDGE, R. J., WILLIAMS, M., VANDENBROUCKE, T. R. A. & ZHANG, K.-G. (2013). Earliest chitinozoans discovered in the Cambrian Duiyun fauna of China. *Geology* **41**, 191–194.
- SHEN, S.-Z., SHEN, S.-Z., CROWLEY, J. L., WANG, Y., BOWRING, S. A., ERWIN, D. H., SADLER, P. M., CAO, C.-Q., ROTHMAN, D. H., HENDERSON, C. M., RAMEZANI, J., ZHANG, H., SHEN, Y., WANG, X. D., WANG, W., MU, L., LI, W.-Z., TANG, Y.-G., LIU, X.-L., LIU, L.-J., ZENG, Y., JIANG, Y.-F. & JIN, J.-G. (2011). Calibrating the end-permian mass extinction. *Science* **334**, 1367–1372.
- SPEHLING, E. A., CARBONE, C., STRAUSS, J. V., JOHNSTON, D. T., NARBONNE, G. M. & MACDONALD, F. A. (2016). Oxygen, facies, and secular controls on the appearance of Cryogenian and Ediacaran body and trace fossils in the Mackenzie Mountains of northwestern Canada. *Geological Society of America Bulletin* **128**, 558–575.
- SPEHLING, E. A., FRIEDER, C. A., RAMAN, A. V., GIRGIS, P. R., LEVIN, L. A. & KNOLL, A. H. (2013). Oxygen, ecology and the Cambrian radiation of animals. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 13446–13451.
- SPEHLING, E. A., KNOLL, A. H. & GIRGIS, P. R. (2015). The ecological physiology of Earth's second oxygen revolution. *Annual Review Ecology Evolution Systematics* **46**, 215–235.
- SPEHLING, E. A., WOLOCK, C. J., MORGAN, A. S., GILL, B. C., KUNZMANN, M., HALVERSON, G. P., MACDONALD, F. A., KNOLL, A. H. & JOHNSTON, D. T. (2015). Statistical analysis of iron geochemical data suggests limited late Proterozoic oxygenation. *Nature* **523**, 451–454.
- SUN, Y., SUN, Y., JOACHIMSKI, M. M., WIGNALL, P. B., YAN, C., CHEN, Y., JIANG, H., WANG, L. & LAI, X. (2012). Lethally hot temperatures during the Early Triassic greenhouse. *Science* **338**, 366–370.
- THOMPSON, J. B., MULLINS, H. T., NEWTON, C. R. & VERCOUTERE, T. (1985). Alternative biofacies model for dysaerobic communities. *Lethaia* **18**, 167–179.
- TOSTEVIN, R., WOOD, R., SHIELDS, G. A., POULTON, S. W., GUILBAUD, R., BOWYER, F., PENNY, A. M., HE, T., CURTIS, A., HOFFMANN, K.-H. & CLARKSON, M. O. (2016). Low-oxygen waters limited habitable space for early animals. *Nature Communications* **7**, 12818.
- TOWE, K. M. (1970). Oxygen-collagen priority and the early metazoan fossil record. *Proceedings of the National Academy of Sciences of the United States of America* **65**, 781–788.
- TRUBOVITZ, S. & STIGALL, A. L. (2016). Synchronous diversification of Laurentian and Baltic rhynchonelliform brachiopods: implications for regional versus global triggers of the Great Ordovician Biodiversification Event. *Geology* **44**, 743–746.
- TWEEDT, S. M. & ERWIN, D. H. (2015). Origin of metazoan developmental toolkits and their expression in the fossil record. In *Evolution of Multicellularity* 44–77 (eds I. RUIZ-TRILLO and A. M. NEDELICU). Springer, The Netherlands.
- TWITCHETT, R. J. (2007). The Lilliput effect in the aftermath of the end-Permian extinction event. *Palaeogeography, Palaeoclimatology, Palaeoecology* **252**, 132–144.
- TWITCHETT, R. J., KRYSSTYN, L., BAUD, A., WHELEY, J. R. & RICHOSZ, S. (2004). Rapid marine recovery after the end-Permian mass extinction event in the absence of marine anoxia. *Geology* **32**, 805–808.
- URBANEK, A. (1993). Biotic crises in the history of Upper Silurian graptoloids: a paleobiological model. *Historical Biology* **7**, 29–50.
- VALENTINE, J. W. & ERWIN, D. H. (1987). Interpreting great developmental experiments: the fossil record. In *Development as an Evolutionary Process* (eds R. A. RAFF and A. R. LISS), 71–107. Alan R. Liss, New York, USA.
- VAN DER LAND, J. (1970). Systematics, zoogeography and ecology of the Priapulida. *Zoologische Verhandlungen* **112**, 1–118.
- VAQUER-SUNYER, R. & DUARTE, C. M. (2008). Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 15452–15457.
- VERON, J. E. N. (1995). *Corals in Space and Time*. Cornell University Press, New York.
- VINTHER, J. (2015). The origins of molluscs. *Palaeontology* **58**, 19–34.
- WADE, B. S. & TWITCHETT, R. J. (2009). Extinction, dwarfing and the Lilliput effect. *Palaeogeography, Palaeoclimatology, Palaeoecology* **284**, 1–3.
- WAGNER, G. P. (2014). *Homology, Genes, and Evolutionary Innovation*. Princeton University Press Princeton, New Jersey.
- WEBBY, B. D., PARIS, F., DROSER, M. L. & PERCIVAL, I. G. (2004). *The Great Ordovician Biodiversification Event*. Columbia University Press, New York.
- WHITE, B. N. (1987). Oceanic anoxic events and allopatric speciation in the deep sea. *Biological Oceanography* **5**, 243–259.
- WOOD, R., IVANTSOV, A. Y. & ZHURAVLEV, A. Y. (2017). First macrobiota biomineralization was environmentally triggered. *Proceedings of the Royal Society of London, Series B* **284**, 20170059.
- WOOD, R. & ZHURAVLEV, A. Y. (2012). Escalation and ecological selectivity of mineralogy in the Cambrian Radiation of skeletons. *Earth-Science Reviews* **115**, 249–261.
- WOOD, R. A., POULTON, S. W., PRAVE, A. P., HOFMANN, K.-H., CLARKSON, M. O., GUILBAUD, R., LYNE, J. W., TOSTEVIN, R., BOWYER, F., PENNY, A. M., CURTIS, A. & KASEMANN, S. A. (2015). Dynamic redox controls Ediacaran metazoan communities in the Nama Group, Namibia. *Precambrian Research* **261**, 252–271.
- XIANG, L., SCHOEPPER, S. D., SHENA, S.-Z., CAO, C.-Q. & ZHANG, H. (2017). Evolution of oceanic molybdenum and uranium reservoir size around the Ediacaran-Cambrian transition: evidence from western Zhejiang, South China. *Earth and Planetary Science Letters* **464**, 84–94.
- ZHURAVLEV, A. Y. (2001). Biotic diversity and structure during the Neoproterozoic-Ordovician transition. In *The Ecology of the Cambrian Radiation* (eds A. Y. ZHURAVLEV and R. RIDING), 536 pp. Columbia University Press, New York.
- ZHURAVLEV, A. Y. & WOOD, R. A. (2009). Controls on carbonate skeletal mineralogy: global CO₂ evolution and mass extinctions. *Geology* **37**, 1123–1126.

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